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## ECOLOGY OF THE WILLOW CONE GALL.

ROY L. HEINDEL.

AMONG the numerous galls to be found everywhere, the cone galls of the willows are very common forms. A little has been done toward their knowledge by Walsh, who has dealt more particularly with descriptions of the galls and their makers and has done little more than make casual mention of ecological relations. An examination of the galls in fall or winter shows them to be the abiding place of the larvæ of a goodly number of insects: Walsh says: "Nothing gives us a better idea of the prodigious exuberance of insect life, and of the manner in which one insect is often dependent upon another for its very existence, than to count up the species which haunt, either habitually or occasionally, one of these willow-galls, and live either upon the substance of the gall itself or upon the bodies of other insects that live upon the substance of the gall."

In the following pages will be discussed, first, the galls themselves, second, the gall makers, and third, the guests and parasites that inhabit the galls.

## THE CONE GALLS.

As is well known, a gall is some abnormal growth of a plant tissue resulting from an external stimulus. In the case of the cone galls and of the other bud galls of the willow the stimulus is furnished by the gall gnat. Whether it is given by the insertion of the ovipositor into the bud, by the presence of the egg, or by the larvæ, I cannot say. The gall attains its full growth by midsummer thus giving evidence of considerable stimulation. Regularity and symmetry in the shape of the gall can be accounted for by the stimulus, whatever it may be, acting equally in every direction.

As a result of this stimulus, the bud takes on a remarkable

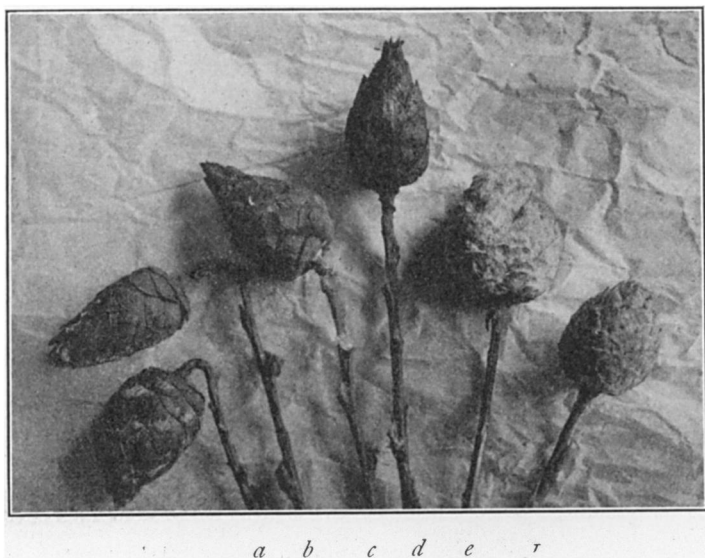


FIG. 1.—Cone gall of *Salix*. *a, b, c, Salicis gnaphaloides* (showing variation in crook of stem); *d, Salicis strobiliscus*; *e, f, Salicis strobiloides*.

activity in growth, and develops a large number (60–75) of scales. These scales are placed in regular order, with their edges overlapping, and form in the center an elongate cell. This cell, protected by the numerous layers of scales, is the abiding place of the gall maker during its larval and pupal stages.

The three cone galls on which I have based most of my study are all found in the vicinity of Lake Forest, Illinois. I also gathered some material in southwestern Wisconsin. They are formed from apical buds. In structure and appearance they are much alike but they have some characteristic differences. The three are :—

1. A pubescent gall found growing on *Salix cordata* Muhl., which corresponds in every particular to the gall found by Walsh on the same willow. This is the gall *Salicis strobiloides* O. S. (Fig. 1, *e* and *f*). It is usually somewhat spherical but occasional galls have the central scales prolonged into a loose tip. It is the dense silvery pubescence which distinguishes this gall most clearly from the others.

2. A cone gall usually more tapering than the above and lacking the dense pubescence. Its marked characteristic is a decided curve or bend in the twig just beneath the gall (Fig. 1, *a*, *b*, *c*). In every respect the gall corresponds to *Salicis gnaphaloides* Walsh, but in no case have I found it on *Salix humilis*, the willow to which Walsh accredits it. Instead, I have found it in great abundance on *Salix bebbiana*.

3. A gall corresponding exactly to *Salicis gnaphaloides*, except that the twig is straight (Fig. 1, *d*), was also found on *Salix bebbiana*, the *Salix rostrata* of Walsh's paper. These galls were not in such great abundance and were usually to be found on the same plant with the gall *S. gnaphaloides*. In some two or three cases small shrubs bearing only a few galls had all straight-stemmed ones. On one shrub with 37 galls, 9 were straight and 28 were crooked. From another clump of willows (*S. bebbiana*) I gathered 65 galls, of which 57 were crooked and only 8 straight. In both cases there was a gradation in the matter of the crook.

Since I shall show a little farther on that these three galls have the same maker, it is evident that the distinction between the first and the others may be due to the peculiar reactions of the different willows to the stimulus which causes the growth of the gall. But in the case of the two galls on *S. bebbiana* the cause of the difference does not seem so clear. It will be necessary to observe the beginning of the gall to see if this can be determined.

In his *Origin of Floral Structures*, Henslow has drawn an analogy between the gall and the flower. He intimates that the gall is the result of the shortening of the axis due to puncturing in the depositing of eggs by insects, and thus represents a lessened growth of twig. I believe that the gall does not represent a shortening of the axis, but, on the other hand, represents a special growth of scales in addition to the normal growth of twig. I base my belief on the following observations:—

1. The scales of the gall have not the normal leaf arrangement or venation. From a single clump of willows (*S. bebbiana*) I gathered a number of twigs and galls. The lateral buds of this willow have the two fifths arrangement. If the gall represents a shortening of the axis the scales ought to show some such arrangement, allowing for a reasonable amount of displacement owing to crowding. While the general arrangement of the scales was in whorls, some showed a spiral arrangement but never the two fifths. I examined in detail about a dozen galls to determine this. Moreover the scales do not very much resemble the leaves of the willows. They differ in shape and margin and show little or no venation and never the venation of the leaf.

2. The gall-bearing shoot is oftenest longer than the non-gall-bearing and develops more lateral buds. From this same bunch of twigs I took 28 bearing the crooked galls and the same number of non-gall-bearing twigs. The average number of lateral buds to the gall-bearing twigs was 20, while the average to the non-gall-bearing twigs was only  $16\frac{1}{4}$ . Eleven gall-bearing and ten non-gall-bearing twigs were taken from the same part of the plant, having had, as nearly as could be determined, the same conditions of growth. The former had an average of  $17\frac{4}{11}$  lateral buds and an average length, from origin of the twig to the base of the gall, of 6.84 inches, and the latter had an average of 17 lateral buds and an average length to base of terminal bud of 6.825 inches. In every case the twigs were of 1904 growth. General observations of various clumps of willows confirmed the foregoing results. However, in one case the average length of five pubescent gall twigs (*Salix cordata*) was 1.13 inches less than the average length of seven non-gall-bearing

ing twigs growing under similar conditions. The former averaged three more lateral buds to a twig than the latter. From another clump of willows 14 twigs bearing pubescent galls had an average of three buds fewer than 14 non-gall-bearing twigs (15 and 18) but the average length was equal.

I conclude that the gall does not represent a shortening of the axis and that the gall-bearing twig does not represent a lessened growth, but that, on the other hand, the gall-bearing

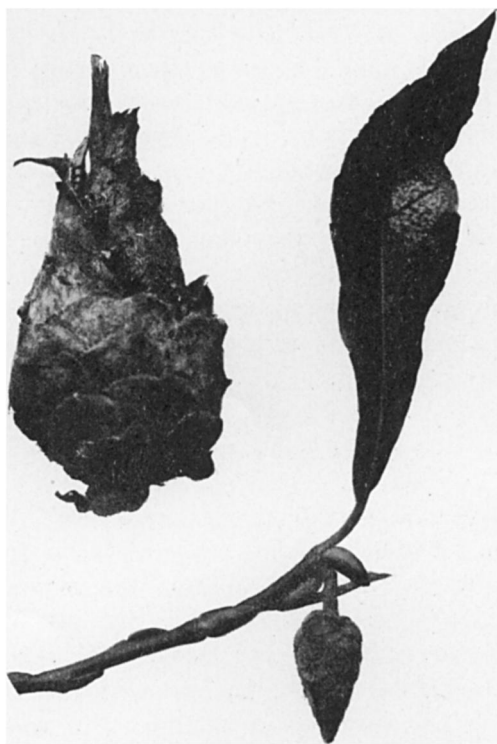


FIG. 2.—Two cone galls showing extremes in size. The larger shows protruding pupal skins of the moth *Acleris*. At the base of the crooked stem of the smaller is a bud favorably placed for continuing growth in a direct line.

twig holds its own with the non-gall-bearing and has in addition the abnormal growth of the gall.

The very abnormal shape of the stem of the crooked gall suggests a question as to its purpose. Since the gall terminates the twig and prevents further apical growth, future growth must

be by means of a branch originating on the twig below the gall. At first it appears as if the crook in the stem (see Fig. 2) might provide for a direct growth by means of a branch from the convex side of the stem. Dr. P. Speiser claims that a bend in the stem is of advantage in this way in the gall *Dichelomyia rosaria* H. Lw., since the gall is turned aside, and thus permits a more or less direct growth from a bud below it. An examination of any willow bearing these crooked galls (*S. gnaphaloides*) shows very plainly that the benefit for continued growth is accidental rather than habitual. To be of service it would be necessary that a bud be located just at the beginning of the crook in the stem. In one lot of 57 galls, 32 had buds so located and 25 were without bud in a favorable position. By watching the willows for further information, I found that very frequently the favorably placed bud either does not develop or sends off a branch at an angle from the parent twig. And just as frequently, when there is no bud so favorably located, a bud farther down, or one immediately beneath the gall, is the one which sends out the most vigorous branch, whose direction is determined by its surroundings.

#### THE GALL MAKERS.

The life history of the gall gnat is very simple. In the spring the larva which has spent the winter in its cell in the gall transforms into the pupa and that, a little later, into the gall gnat itself. The gnats soon deposit their eggs in apical buds of willows. From the eggs larvæ are hatched and the cycle begins again. Walsh speaks of observing larvæ as late as April 23, and pupæ from early in April until late in May. From galls gathered and examined on the following dates I found larvæ of the gall gnats: October, November 12, December 26, January 17, February, about March 20, and the first and second weeks of April. In March and April, many larvæ were almost ready for transforming into pupæ but only a few pupæ were found. Gnats had emerged from all the galls examined June 3. I kept some of the galls gathered in December and on subsequent dates, to watch for transformations. From those of December 26, one or

two gnats emerged about the middle of February. From those of March 20 several gnats emerged early in April. From the April specimens they began to appear within a week and continued to emerge for over three weeks. Because of the difficulty in rearing gall gnats my data are not complete. But it is evident that the insect exists for a long time in the larval state and that the pupal period is comparatively short.

Walsh found it difficult to devise an artificial mode of treatment for rearing the gall gnats in the house. My results with

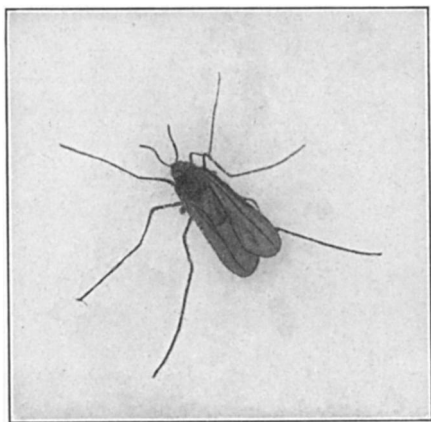


FIG. 3.—Gall gnat (*Rhabdophaga strobiloides* O. S.) enlarged.

the earlier lots of galls were not very successful. At first I threw them in jars and boxes but found that in a short time larvæ and pupæ dried up in many of the galls. Then I tried keeping them with the stems in water but with scarcely better success. With the last lot I used a different plan. I tied the galls in squares of cheese cloth, opening the bundles and sprinkling them every day or two. This plan was very successful. Of course it is possible that the season had something to do with it, for it was nearly the regular time for the emerging of the gnats. But that cannot be the full explanation, for, in packages which were neglected, the results were less satisfactory. The sprinkling seems to have taken the place of the spring showers.

Cecidomyiids offer considerable difficulty in the matter of



specific determination. Walsh has called the maker of each of the fifteen willow galls he describes a distinct species. If the galls themselves could be taken as a means of determining species his results would in most cases stand. Although I have been working with only a few of the cone galls, it is necessary to consider some others in settling this question.

Of Walsh's fifteen willow galls, six are more or less cone-shaped bud galls of somewhat similar structure. The larvæ found and described by Walsh in these six are precisely alike as to size, shape, "breast bone," etc. Walsh gives, however, the following differences in the cocoons:—

*Cecidomyia salicis brassicoides*, cocoon scarcely larger than larva.

*Cecidomyia salicis strobiliscus*, cocoon  $1\frac{1}{2}$  to 2 times as long as larva.

*Cecidomyia salicis gnaphaloides*, cocoon  $1\frac{1}{2}$  to 2 times as long as larva.

*Cecidomyia salicis coryloides*, cocoon 2 times as long as larva.

*Cecidomyia salicis strobiloides*, cocoon  $2\frac{1}{2}$  to 3 times as long as larva.

*Cecidomyia salicis rhodoides*, cocoon  $2\frac{1}{2}$  to 3 times as long as larva.

The difference seems to be considerable but it is easily explained. I have examined all except the fourth (*coryloides*), ten or more galls of each, and have found the length of the cocoons to vary in the different galls in proportion to the length of the central cell or cavity (see Fig. 5). The gall *S. brassicoides* has a short cell which permits of only a short cocoon, while the gall *S. strobiloides* has a long central cell giving plenty of space for a long cocoon. If the cocoon is exuded from the larva and is expanded by a gas, as Walsh supposed, then the length and size of the central cell certainly would determine the size of the cocoon.

In these same six species Walsh found the pupæ of only five. The only difference I can find in his descriptions is that *C. s. gnaphaloides* (in dried specimens) is slightly shorter than the others. I could not find this difference.

From a careful comparison of Walsh's descriptions and from

verifications by observation in the case of the cocoons of five of the galls and in the case of the larvæ and pupæ of three of them, I am convinced that specific differences, if any, must be looked for in the imagoes, for they cannot be found in the earlier stages.

Imagoes of the makers of five bud galls were found and described by Walsh. I give below a table showing the differences which he finds in them.

*Imagoes of Bud Gall Makers.*

Species	<i>brassicoides</i>	<i>strobiloides</i>	<i>strobiliscus</i>	<i>gnaphaloides</i>	<i>rhodoides</i>
Antennal Joints	22-24	21-22	23-24		21-25
Thoracic Hairs	Dusky	Whitish	Whitish	Whitish	Whitish
Length in Inches	0.16-0.20	0.16-0.20	0.16-0.20	0.12-0.15	0.16-0.20
Origin of Anterior Branch of Cubital Wing Vein	Occasionally obsolete	Always obsolete for a short space	Rather distinct	Rather distinct	Occasionally obsolete

The variation in the number of antennal joints makes that feature useless as a specific characteristic. Antennæ of dried specimens are easily broken, but by using fresh and alcoholic specimens, I find that there are about the same number of joints in those of all the gnats which make the different galls.

The color of thoracic hairs is the first and only distinguishing characteristic. I have had only five imagoes of *C. s. brassicoides* Walsh but find that the dusky hairs are present in all, while in the gnats from the four other galls the thoracic hairs are whitish.

Length shows no difference except in the one case, and I think this cannot be considered for I found four, from one lot of five imagoes from the gall *S. gnaphaloides*, which were fully 0.21 inches in length, and I have found but one or two as short as 0.12 inches.

As to wing venation the wings of four *C. s. brassicoides* Walsh have the origin of the anterior branch of the cubital vein distinct. Seventeen left and eighteen right wings of *C. s. strobiloides* Walsh gave the following results as to the origin of the anterior branch of the cubital vein:—

Origin of 16 anterior veins obsolete.

Origin of 6 anterior veins very indistinct, probably obsolete.

Origin of 4 anterior veins indistinct, probably not obsolete.

Origin of 9 anterior veins distinct.

These results do not agree with Walsh's statement but, on the contrary, show that this feature of the wing venation cannot be taken as a specific characteristic. Wings of five *C. s. gnaphaloides* Walsh and two *C. s. strobiliscus* Walsh have the

origin of the anterior branch very distinct. Four *C. s. rhodoides* Walsh show it "occasionally obsolete" as given by Walsh. The fact that variations do occur and that each of the so called species has some individuals with the venation like that of other species is sufficient to throw this out as a determining characteristic. Walsh says him-

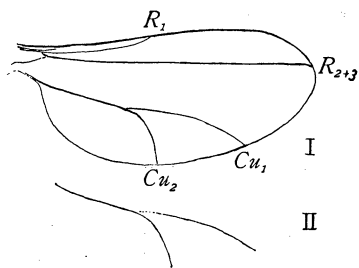


FIG. 4.—Wing venation of gall gnat.  $Cu_1$ , Anterior branch of cubitus. I. Origin distinct II. Origin obsolete.

self that the imagoes of his *gnaphaloides* and *rhodoides* are indistinguishable except for size, and I have shown that this difference is not fixed.

His *brassicoides* differs from the others in having dusky instead of whitish thoracic hairs. Since the few specimens I have had showed this same difference, it is necessary, at least until other material is available, to let *C. brassicoides* stand as a distinct species. But from the data I have given and from the comparison I have made of Walsh's descriptions with each other and with my specimens, I must conclude that *strobiloides*, *strobiliscus*, *gnaphaloides*, and *rhodoides* are synonymous. Since the first name was given by Osten Sacken in 1861, I have taken it as the name of the species and the three others as synonyms. So the gnat which produces the four galls, *Salicis strobiloides*, *Salicis strobiliscus*, *Salicis gnaphaloides*, and *Salicis rhodoides* is *Rhabdophaga strobiloides* O. S. This verifies the inference of Bergenstamm and Löw that Walsh's species are all *strobiloides*.

Summarizing, *Rhabdophaga strobiloides* O. S. produces : gall

*Salix strobiloides* on *Salix cordata*; gall *Salix strobiliscus* on *Salix bebbiana*; gall *Salix gnaphaloides* on *Salix bebbiana*; gall *Salix rhodoides* on *Salix humilis*.

#### GUESTS AND PARASITES.

While I was gathering material for the study of the gall gnat I bred as many as possible of the other insects which inhabit the galls. These include not only the inquilines and the transient guests, but also a number of parasites which live on these inquilines or on the gall maker.

In making my table of results I have included a few species bred by Professor J. G. Needham from cone galls and from the galls *S. rhodoides* and *S. brassicoides* during the spring of 1904.

#### List of Insects bred from Galls.

	Gall <i>S. strobiloides</i>	Gall <i>S. gnaphaloides</i>	Gall <i>S. strobiliscus</i>	Gall <i>S. rhodoides</i>	Gall <i>S. brassicoides</i>
Gall makers:					
<i>Rhabdophaga strobiloides</i> O. S. . . . .	×	×	×	×	
<i>Rhabdophaga brassicoides</i> Walsh . . . . .					×
Inquilines:					
<i>Cecidomyia albovittata</i> Walsh . . . . .	×	×	×		
<i>Chaitophorus</i> sp. (plant louse) . . . . .	×	×	×		
<i>Pontania pisum</i> Walsh (saw fly) . . . . .	×	×	×		
<i>Euura noda</i> Walsh (saw fly) . . . . .	×	×	×		
<i>Xiphidium ensiferum</i> , eggs (meadow grasshopper) . .	×	×	×		
A spring-tail ( <i>Thysanura</i> ) . . . . .	×	×	×		
<i>Acleris heindelana</i> Fernald (a moth) . . . . .		×			
Larvæ of a Noctuid (Lepidoptera) . . . . .		×	×		
Larva of Tineid (?) (Lepidoptera) . . . . .		×			
Larva of <i>Thyridopteryx ephemeraformis</i> (?) (Lepidoptera) . . . . .		×			
Parasites and hyperparasites:					
<i>Tetrastichus</i> sp. . . . .	×	×			×
<i>Tetrastichus</i> sp. . . . .	×	×			×
<i>Tetrastichus</i> sp. . . . .	×	×			×
<i>Polygnotus salicicola</i> Ashm. (a Proctotrupid) . . .	×	×			×
<i>Eurytoma studiosa</i> Say (a Chalcid) . . . . .	×	×			×
<i>Pteromalus</i> sp. (a Chalcid) . . . . .	×		×		
<i>Torymus popenoi</i> Ashm. (a Chalcid) . . . . .	×				×
<i>Aphanogmus virginianensis</i> Ashm. . . . .	×	×			

*Lists of Insects bred from Galls. (Continued.)*

	Gall <i>S. strobiloides</i>	Gall <i>S. gnaphaloides</i>	Gall <i>S. strobiliscus</i>	Gall <i>S. rhododes</i>	Gall <i>S. brassicoides</i>
<i>Aphelinus mytilaspidus</i> Le Baron (a scale parasite) . . . . .		×		×	
A Campoplegine . . . . .	×				
An Encyrtine . . . . .	×				
<i>Copidosoma intermedium</i> How. . . . .	×				
<i>Urogaster forbesii</i> Ashm. . . . .	×				
<i>Tridymus metallicus</i> Ashm. . . . .		×			
<i>Dapanus</i> n. sp. (an Ichneumonid) . . . . .	×				
<i>Oncophanes</i> n. sp. (a Braconid) . . . . .	×				
Transient and accidental guests:					
<i>Megalothrips</i> sp. . . . .	×				
<i>Phlaothrips</i> sp. . . . .	×				
<i>Ischnorhynchus resedæ</i> Panzer (Heteroptera) . . . . .	×				
<i>Triphleps insidiosus</i> Say (Heteroptera) . . . . .		×			
A pseudoscorpion . . . . .		×			

Thus we find at least 32 species of insects making use of the cone galls. Of these, one is a gall maker, 10 are inquiline, 16 are parasites or hyperparasites, and 5 are transient or accidental guests. It will be noticed that the greater number are from *S. strobiloides*, which may be due to the better protection offered by the dense pubescence. The larger insects were more numerous than small ones in *S. gnaphaloides*.

The following description of the moth bred from the gall *S. gnaphaloides* has been furnished for publication in this paper by Professor C. H. Fernald:—

***Acleris heindelana* Fernald n. sp.**

Expanse of wings, 15–17 mm. Head, thorax, and fore wings dull steel gray, the wings with a trace of light brown stain below the large triangular dark brown costal spot which extends from the basal third to near the outer fifth of the costa and about halfway across the wing. This spot has minute scattered tufts of blackish scales over the surface and there are also a few other blackish scale tufts in places common to the species of this genus.

Fringes concolorous with the adjoining surface of the wing. Hind wings pale gray with a silky luster, a little darker at the apex, and with the fringes of the same color as the base of the wings. Under side of the fore wings much darker than the hind wings and with the costa marked alternately with light and dark gray. The hind wings are sprinkled with brown dots towards the apex. Abdomen of the same color as the hind wings.

Described from two female specimens: one from Lake Forest, Ill., and one belonging to the U. S. National Museum and taken in Winnipeg, Manitoba, by A. W. Hanham.

I have one specimen in rather poor condition which may possibly belong to this species. It is labeled as follows: "Ft. Klamath, Ore., 10.6. '86. T. C. M. Coll."

Eggs of the meadow grasshopper (*Xiphidium ensiferum*) were found in both old and recent galls. In many cases they were dried up. The grasshoppers began to appear in May. Wheeler says that the meadow grasshoppers seem to prefer the blackened and weatherbeaten galls, probably because their scales are more easily forced apart. He believes that this insect's habit of putting its eggs in the galls is of comparatively recent acquisition because in some cases the eggs are poorly placed and because the insect still uses galls whose scales are so close together as to flatten and kill the eggs, evidence that the grasshopper has not learned to distinguish the kind of gall best adapted to its purpose. If we accept Wheeler's conclusion, we may say that the gall is of increasing importance to the insect world.

So far as is known, *Tetrastichus* is hyperparasitic. There are numerous undescribed species which are difficult to separate.

*Polygnotus salicicola* was bred from a Cecidomyiid leaf gall of the willow by Mr. A. Koebele at Los Angeles, Cal.

Mr. Theo. Pergande says that both of the thrips, *Megalothrips* and *Phlæothrips*, are apparently undescribed.

*Ischnorhynchus resedæ* Panzer is a common European species, also common in the United States. *Triphleps insidiosus* Say is a common and widespread species found upon berries and upon the ox-eye daisy.

Although it is difficult and often impossible to identify the various insects in their larval state, still an early examination is of value for showing the abundance of life in the individual galls. Usually the larva of the gall gnat which is the maker of the gall,

is present in its central cell. It is easily recognized, not only by its larger size, but especially by the presence of the "breast bone" so characteristic of all Cecidomyiid larvæ. Larvæ of small Cecidomyidæ are found in considerable numbers between the outer scales of many galls.

These are also recognized by the "breast bone" but with greater difficulty because of their smaller size.

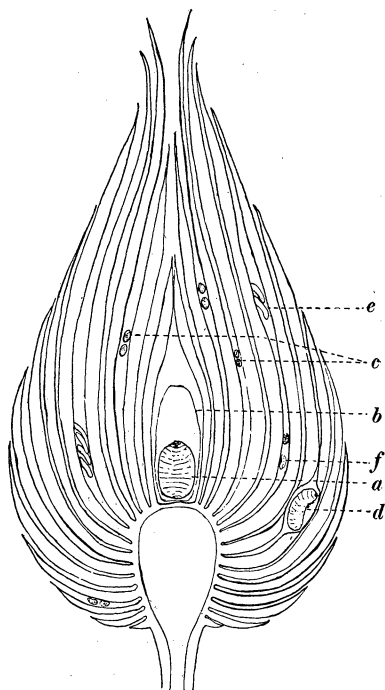


FIG. 5.—Diagrammatic drawing of section of a cone gall, showing positions of gall makers and others. *a*, Rhabdophaga larva; *b*, its cocoon; *c*, guest Cecidomyiid larvæ; *d*, saw fly or moth larva in a burrow; *e*, eggs of *Xiphidium ensiferum*; *f*, larva of Hymenopterous parasite.

gnats, 1 guest Cecidomyiid about half as long as the gall maker, 37 smaller Cecidomyiid larvæ, 2 parasitic larvæ, and 13 grasshopper eggs. Six 1903 galls from same place contained 32 grasshopper eggs.

Seventeen 1904 crooked-stem galls from west of Lake Bluff Ill., gathered January 17, 1905, contained ten larvæ of the gall maker, 28 Cecidomyiid larvæ about half as large as maker, 10

Twenty-three 1904 pubescent galls from the region of Pettibone Creek, north of Lake Bluff, Ill., gathered and examined in October, 1904, contained fifteen living and two dead larvæ of the gall gnat which produces the gall (6 galls were without Rhabdophaga larvæ), 169 small Cecidomyiid guest larvæ, 6 larvæ of Hymenopterous parasites of which two were in the central cell of one gall in place of the Rhabdophaga larva, and 384 meadow grasshopper eggs. One 1903 gall from the same place contained 16 grasshopper eggs.

Nine 1904 pubescent galls from South Wayne, Wis., gathered December 26, 1904, contained 9 larvæ of gall

smaller Cecidomyiid larvæ, 5 saw fly larvæ, 13 larvæ of Hymenopterous parasites, and nearly 400 grasshopper eggs. Three 1903 galls from same place contained 3 saw fly larvæ and about 125 grasshopper eggs.

I can conclude with no more appropriate words than those which Walsh used in connection with another gall: "If this one little gall and the insect which produces it were swept out of existence, how the whole world of insects would be convulsed as by an earthquake! How many species would be compelled to resort for food to other sources, thereby grievously disarranging the due balance of insect life! How many would probably perish from off the face of the earth, or be greatly reduced in numbers! Yet to the eye of the common observer this gall is nothing but an unmeaning mass of leaves, of the origin and history of which he knows nothing and cares nothing!"

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